PARASITIZATION OF BRITISH LADYBIRDS BY DINOCAMPUS COCCINELLAE (SCHRANK) (HYMENOPTERA: BRACONIDAE)

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The braconid wasp, Dinocampus coccinellae (Schrank) is perhaps the best known parasitoid of British coccinellids. The species is a member of the subfamily Euphorinae (see Shaw & Huddleston, 1991, for general biology of the subfamily). The life history of this wasp has been well documented (Ogloblin, 1924; Balduf, 1926; Bryden & Bishop, 1945; Walker, 1962; Sluss, 1968; Maeta, 1969; Hodek, 1973; Obrycki et al., 1985; Majerus, 1991, 1994). In brief, D. coccinellae is a thelytokous parthenogen, female offspring resulting from unfertilized eggs, males being generally absent. The wasp specializes in parasitizing coccinellids, attacking a wide range of host species. Adult wasps lay a single egg into adult or, less frequently, larval or pupal hosts. Although several females may lay in the same host individual, only a single larva develops per host, first instar larvae being equipped with large mandibles which are used to kill other eggs and larvae in their host. Larvae feed on trophic cells (teratocytes) which erupt into the body of the host when the egg hatches (Ogloblin, 1924: Sluss, 1968: Kadono-Okuda et al., 1995). These cells swell, absorbing nutrients from the host. Once fully developed the larva exits, usually through the ventral surface of the host's abdomen, and spins a silken cocoon between the legs of its host. anchoring it to the substrate. In Britain, D. coccinellae has two or three generations per year and passes the winter as a larva within its host.

Despite the considerable amount of documentation on the life history of this parasitoid, there are rather few reports of the levels of parasitization on different coccinellid species. Hodek (1973) states that parasitization rates vary considerably according to region, season and the host. He sensibly contends that comparison of data from the literature is of little value because of differences in the methods used to ascertain parasitization levels. Some rates are determined by dissection while others are assessed by observing the number of parasitoid larvae that successfully emerge from their hosts. Furthermore, some data sets omit crucial details such as the date that samples were collected, the treatment of samples after collection, and even the total number of individuals in samples. Reviewing available data, Hodek (1973) cites parasitization levels of *D. coccinellae* in ten host species. Rates of infestation vary from levels of around 1% to a maximum of 38% recorded for *Coccinella septempunctata brucki* Muls. in Japan (Maeta, 1969). The only British data cited by Hodek report 20% parasitization of *Coccinella septempunctata* L. in Berkshire (Walker, 1962).

Here I report parasitization rates for *D. coccinellae* in samples of a number of British coccinellids collected between June 1984 and May 1996.

METHODS

Samples of coccinellids of various species were collected in one of three ways, by eye (E), by use of a beating tray (B) or by use of a sweep net (S). The status of adults with respect to activity and generation was assessed, division being made into six

categories: overwintering (W), overwintered reproducing (R), new generation reproducing (N), new generation preparing for winter (P), mixed generation active (M) and aestivating (A). The collection of samples was unsystematic with respect to geographic region. The majority were collected in southern England or East Anglia, but most parts of the British mainland yielded some samples. Samples were transferred to 90-mm Petri dishes usually on the day of collection, and always within four days of collection, and retained in the laboratory at around 21°C. Ladybirds were fed suitable food. For predatory species, aphids of three species (Acyrthosiphon pisum (Harris), Aphis fabae Scop. and Microlophium carnosum Buckton) were used as available, together with an artificial agar-based food (see Majerus et al., 1989 for recipe). Non-predatory species were fed on artificial food only.

Samples were examined daily for emerging parasitoid larvae. Samples were retained for at least 50 days. In no case did parasitoid larvae emerge from ladybirds more than 33 days after collection. Details of the number of parasitized and unparasitized ladybirds were recorded for all samples including those from which no parasitoids were found. It should be noted that due to the methods used (samples were not dissected), the results obtained only give levels of successful parasitization,

not of attacks.

RESULTS

Table 1 gives details of the parasitization levels in all samples in which the sample size exceeded the arbitrary figure of 20 individuals. Table 2 summarizes the results for all samples of each species.

DISCUSSION

The results lead to a number of very general conclusions. In Britain, D. coccinellae parasitizes a wide range of coccinellid hosts, but by no means all species. Taking the total sample sizes into account, it seems reasonable to conclude that Anisosticta 19punctata (L.), Adalia 2-punctata (L.) and Exochomus 4-pustulatus (L.) are not successfully parasitized by D. coccinellae in Britain. In addition, it seems probable that Subcoccinella 24-punctata (L.), Aphidecta obliterata, (L.), Adalia 10-punctata (L.), Myrrha 18-guttata (L.), Thea 22-punctata (L.), Chilocorus renipustulatus (Scriba) and Chilocorus 2-pustulatus (L.) are rarely, if ever, successfully attacked. With regard to S. 24-punctata, a member of the sub-family Epilachninae, lack of parasitization is in accord with the contention (Balduf, 1926; Liu, 1950) that Epilachninae are never parasitized by D. coccinellae. Similarly, the data from the two species of Adalia support the view that species of this genus are immune to successful attack. It may be noted that several authors (Bryden & Bishop, 1945; Walker, 1962; Klausnitzer, 1969) report that D. coccinellae readily attack the adults of Adalia species in captivity, but that parasites never emerge, and the ladybirds do not appear to suffer. The lack of parasitization in any of the three British species of the sub-family Chilocorinae also supports previous reports, for no members of this sub-family are included in Hodek's (1973) list of the host species of this wasp. However, Hodek (1973) does include an unpublished data set of parasitization of coccinellids in northern Transvaal which gives a parasitization level of 6.6% of Exochomus concavus Fürsch by D. coccinellae (van Rensburg, unpublished).

Of the British species that are parasitized by this wasp, *Coccinella 11-punctata* L. (22.1%), *Harmonia 4-punctata* (Pont.) (19.4%) and *C. 7-punctata* (17.4%) are the only species to suffer high levels of parasitization reasonably consistently, although

Table 1. Details of samples of adult ladybirds collected and retained to allow the emergence of parasitoids. (For abbreviations, see text.)

Species	Date	Location (given as O/S ref.)	method and adult status	Sample size	Number infected	Infection rate (%)
S. 24-punctata (L.)	19.x.87	TL820900	S-W	168	0	0
24-spot ladybird	15.vi.88	TL820900	S-R	48	0	0
	15.i.89	SZ175905	S+B-W	81	0	0
	12.vi.95	TL817729	S-R	56	0	0
T. 16-punctata (L.)	8.i.86	TL752760	B - W	127	3	2.4
16-spot ladybird	18.x.86	TL817729	B + S - W	563	7	1.2
	18.x.86	TL752760	B + S - W	164	4	2.4
	18.x.86	TL395629	S-W	344	12	3.5
	14.xi.86	SU163057	S-W	187	5	2.7
	9.xii.86	TL760825	S-W	931	13	1.4
	10.xii.86	TL519588	B+S-W	423	8	1.9
	17.iii.87	TL817729	B+S-W B+S-W	1776 1191	15 12	0.8 1.0
	17.iii.87 18.iii.87	TL752760 TL395629	S-W	178	2	1.0
	25.iii.87	SU163057	S-W	93	0	0
	25.x.87	TL817729	B+S-W	169	4	2.4
	25.x.87	TL752760	B+S-W	100	2	2.0
	25.x.87	TL395629	S-W	428	11	2.6
	17.xii.87	TQ180525	B+S-W	241	1	0.4
	14.i.88	SP437091	S-W	279	4	1.4
	13.iii.88	TL817729	B+S-W	1085	9	0.8
	13.iii.88	TL752760	B + S - W	629	7	1.1
	13.iii.88	TL395629	B+S-W	242	0	0
	21.x.88	TL817729	B+S-W	155	3	1.9
	21.x.88	TL752760	B+S-W	158	4	2.5
	21.x.88	TL395629	S-W	272	13 2	4.8
	15.iii.89 15.iii.89	TL817729 TL752760	B+S-W B+S-W	271 337	2	0.7 0.6
	15.iii.89	TL395629	S-W	194	5	2.8
Adonia vanico ata			E+S-M		3	2.7
Adonia variegata (Goeze) Adonis' ladybird	8.viii.91	SJ989185	E+S-M	113	3	2.1
A. 19-punctata (L.)	5.vi.85	SU019562	E+B-R	43	0	0
Water ladybird	6.xi.87	TL416616	E-W	1276	0	0
·	1.ix.88	TQ185605	E+B-P	62	0	0
A. obliterata (L.)	16.vii.86	NN970536	B-M	89	0	0
Larch ladybird	8.ix.86	TL141437	B-P	121	0	0
	14.xi.94	TL817729	E+B-W	44	0	0
A. 2-punctata (L.)	5.i.87	TL444586	E-W	122	0	0
2-spot ladybird	7.iii.87	TL444586	E-W	89	0	0
· ·	5.v.87	TL444586	E-R	267	0	0
	11.vii.87	TL444586	E-N	354	0	0
	9.ix.87	TL444586	E-P	287	0	0
	4.ix.87	TL444586	E-W	134	0	0
	15.i.89	SU163057	E-W	83	0	0
						(Continue

Table 1 (continued)

Species	Date	Location (given as O/S ref.)	Collection method and adult status	Sample size	Number infected	Infection rate (%)
	2.vi.90 26.v.94 14.i.95	SJ816449 TL447576 TL415574	E-R E-R E-W	77 1426 1238	0 0 0	0 0 0
A. 10-punctata (L.) 10-spot ladybird	8.vi.87 11.vii.87 9.ix.87 16.i.89 13.viii.90	TL444586 TL444586 TL444586 SU163057 SX798627	$\begin{array}{c} E-R \\ E-M \\ E-P \\ E-W \\ E-M \end{array}$	34 61 29 21 40	0 0 0 0	0 0 0 0
C. 7-punctata L. 7-spot ladybird	18.x.86 18.x.86 18.x.86 17.iii.87 17.iii.87 18.iii.87 6.vi.87 12.vii.87	TL817729 TL752760 TL395629 TL817729 TL752760 TL395629 TL447576 TL447576	$E + B - W \\ E - R \\ E - M$	879 734 230 765 937 198 113 355	166 191 78 96 120 48 21	18.9 25.6 33.9 12.5 12.8 24.2 18.9 3.9
C. 5-punctata L. 5-spot ladybird	12.v.89 19.xii.90 3.i.93	SN626754 SN626754 SN626754	E+B-R $E+B-W$ $E+B-W$	31 27 55	1 5 5	3.2 18.5 9.1
C. 11-punctata L. 11-spot ladybird	14.xi.86 19.iii.92 17.vi.92 2.ix.92 19.xii.93 13.iii.94	SZ175905 SZ175905 TF730438 TF942440 TL415574 TL415574	$\begin{array}{c} B-W \\ B-W \\ E+B-R \\ E+B-P \\ E-W \\ E-W \end{array}$	53 51 63 44 23 28	18 9 12 13 4 2	34.0 17.6 19.0 29.5 17.4 7.1
C. magnifica Redtenbacher Scarce 7-spot ladybird	12.v.86 11.xi.86 16.iii.89 22.viii.89	SU115034 SU115034 SU115034 SU115034	E+B-R $B-W$ $B-W$ $E+B-W$	44 25 22 188	0 0 0 1	0 0 0 0.5
Coccinella hieroglyphica L. Hieroglyphic ladybird	19.vi.86 9.vi.89	SU994366 SU994366	S-R S-R	199 35	0	0 2.9
H. 4-punctata (Pontoppidan) Cream-streaked ladybird	8.v.88 8.v.88 12.viii.88 15.xii.88 3.iii.89	TL760825 TL817729 TL817729 TL817729 TL817729	$\begin{array}{c} B-R\\ B-R\\ B-P\\ E+B-W\\ E+B-W\end{array}$	42 81 103 31 27	7 13 19 10 6	16.7 16.0 18.4 32.3 22.2
M. 18-guttata (L.) 18-spot ladybird	19.x.87 16.i.89	TL820900 SU307145	E + N - W $E + B - W$	22 35	0	0
Calvia 14-guttata (L.) Cream-spot ladybird	5.vi.84 8.vi.87 11.vii.87 9.ix.87	TL825882 TL444586 TL444586 TL444586	E-R $E-R$ $E-M$ $E-P$	26 28 21 23	1 0 0 3	3.8 0 0 13.0
						(Continued

Table 1 (continued)

Species	Date	Location (given as O/S ref.)	Collection method and adult status	Sample size	Number infected	Infection rate (%)
P. 14-punctata (L.) 14-spot ladybird	29.v.85 8.v.88 7.vi.89 29.xi.89 4.xi.95 14.ii.96	TL825882 TL817729 TL817729 TL817729 TL817729 TL817729	E+S-R E+S-R E+S-R E-W E+S-W E+S-W	124 98 213 84 22 21	0 2 0 7 1	0 2.0 0 8.3 4.5
M. oblongoguttata (L.) Striped ladybird	12.v.86 8.v.88 8.v.88	SU307145 TL760825 TL817729	$\begin{array}{c} B-R \\ B-R \\ B-R \end{array}$	32 47 29	0 2 0	0 4.3 0
A. ocellata (L.) Eyed ladybird	4.vii.84 7.x.84 12.v.86 8.v.88 8.v.88	SU994366 SU994366 SU307145 TL760825 TL817729	E+B-A E+B-P B-R B-R B-R	40 42 57 28 77	1 0 2 0 1	2.5 0 3.5 0 1.3
Halyzia 16-guttata (L. Orange ladybird) 8.v.88 26.v.88 30.vi.89 24.vi.94 27.vi.95	TL817729 TQ173527 TQ173527 TQ173527 TQ173527	$\begin{array}{c} B-R\\ E+B-R\\ E+B-R\\ E+B-R\\ E+B-R\end{array}$	27 147 180 56 80	0 3 0 0 1	0 2.0 0 0 1.3
T. 22-punctata (L.) 22-spot ladybird	19.x.87 21.x.88 14.vii.89	TL820900 TL395629 TL376641	S-W $E+S-W$ $E-W$	43 61 39	0 0 0	0 0 0
C. renipustulatus (Scriba) Kidney-spot ladybird	28.viii.86 16.v.90	SU908587 SP437091	E-P E-R	26 88	0	0
C. 2-pustulatus (L.) Heather ladybird	9.vi.89	SU994336	S-R	46	0	0
E. 4-pustulatus (L.) Pine ladybird	4.vii.84 18.x.86 3.iii.87 21.x.87 1.iii.88 12.xi.88 24.ii.89 7.vi.94 25.xii.94	SU994366 TL817729 TL760825 TL760825 TL760825 TL760825 TL760825 SU307145 TL422567	E+B-N E+B-W E+B-W E+B-W E+B-W E+B-W E+B-W E+B-P	108 548 675 200 494 120 441 216 81	0 0 0 0 0 0 0	0 0 0 0 0 0 0

the scarce (in Britain) ladybird *Coccinella 5-punctata* L. may also suffer significant losses. In the other species infected, parasitization levels were generally below 5%.

Various authors have previously commented upon the possible role that ladybird size may have in determining whether a species is a suitable host for *D. coccinellae*. For example, Klausnitzer (1969) speculates that parasitization of *Anatis ocellata* (L.) by this wasp is impeded by the coccinellid's large size. Conversely, some authors have

Table 2. Mean infestation rates across all samples for each species.

Species	Total of samples	Number parasitized	Mean level of infestation (%)
S. 24-punctata	353	0	0
T. 16-punctata	10537	148	1.4
A. variegata	113	3	2.7
A. 19-punctata	1381	0	0
A. obliterata	254	0	0
A. 2-punctata	4077	0	0
A. 10-punctata	185	0	0
C. 7-punctata	4222	734	17.4
C. 5-punctata	113	11	9.7
C. 11-punctata	262	58	22.1
C. magnifica	279	1	0.4
C. hieroglyphica	234	1	0.4
H. 4-punctata	284	55	19.4
M. 18-guttata	57	0	0
C. 14-guttata	98	4	4.1
P. 14-punctata	562	10	1.8
M. oblongoguttata	108	2	1.9
A. ocellata	244	4	1.6
H. 16-guttata	490	4	0.8
T. 22-punctata	143	0	0
C. renipustulatus	114	0	0
C. 2-pustulatus	46	0	0
E. 4-pustulatus	3444	0	0

contended that the lack of records of successful parasitization of *A. 2-punctata* and *A. 10-punctata* by *D. coccinellae* may be due to the small size of these ladybirds (Hodek, 1973; Majerus & Kearns, 1989). The data presented here must draw these speculations into doubt. In the case of *A. ocellata*, several successful cases of parasitization are noted. In addition, *Myzia oblongoguttata* (L.), which is only marginally smaller than *A. ocellata*, was also successfully attacked. Furthermore, Timberlake (1916) reports the parasitization of the large coccinellid *Olla abdominalis* (Say) by *D. coccinellae*.

The contention that the two British Adalia species are too small to support full development of the parasitoid larva must be doubted on the basis of the findings with respect to Tytthaspis 16-punctata (L.), which is considerably smaller than either Adalia species (and see Majerus, in prep.). Thus, it seems that although host size may play some part in determining the successful reproduction and development of D. coccinellae, it is not the only factor involved, and in some species it is probably not the most crucial one.

Iperti's (1964) assertion that it is difficult, although not impossible, to obtain emergence of adult wasps from cocoons resulting from parasitization of *Propylea 14-punctata* (L.) is not born out by my observations here. All ten of the cocoons from the *P. 14-punctata* samples produced wasps normally.

One other interesting species is *Coccinella magnifica* Red. The results show that all five British species of *Coccinella* are capable of being parasitized, but that *C. magnifica* is rarely successfully infected. This has been found by other workers (Sloggett, pers. comm.). The low level of attack against *C. magnifica* is of interest

partly because it is surprising when compared with other species of its genus, and partly because there is a plausible explanation for the low level of attack. The infestation levels of C. magnifica are much lower than those of C. 7-punctata, yet the two species are closely related and are of a similar size. However, C. magnifica is a myrmecophile, in Britain living exclusively in the vicinity of the nests of wood ants (Formica rufa group sp.) (Donisthorpe, 1920; Majerus, 1989, 1994; Sloggett pers. comm.), while C. 7-punctata is rarely found close to such ants. One of several nonmutually exclusive hypotheses for the causes of the evolution of myrmecophily in C. magnifica is that by living in close proximity to these aggressive ants, the ladybirds gain a natural selective advantage through reduced parasitization and predation (Majerus, 1989, 1994). The essence of this hypothesis is that the ants drive potential predators and parasitoids away from their foraging area. This might account for the low level of infestation by D. coccinellae found. Alternatively, D. coccinellae may itself shun the vicinity of Formica nests, either to avoid harassment by ants, or because the density of coccinellids is low in such areas. It is pertinent to note that no other parasitoid has been recorded from C. magnifica in Britain (Majerus, 1994).

While keeping in mind Hodek's (1973) points in respect of the difficulty of comparing parasitization levels, a number of comparisons can be made, particularly when samples being compared vary only in one detail, such as date, or location. Considering location first, few species show any significant and consistent differences in infestation rates between sites. For some species, the infestation rates found are too small to show such differences given the current sample sizes. One possible exception concerns C. 7-punctata in which samples from Dry Drayton (TL395629) show consistently higher infestation rates than those from two other East Anglian

sites taken at the same time.

More instructive are comparisons between samples taken from the same sites on different dates. Again the results from C. 7-punctata are perhaps most valuable because of the relatively large sample sizes and the high infestation rates. Comparisons of pairs of samples of overwintering beetles, collected from three sites in October 1986 and March 1987, reveal that at all three of the sites the infestation rate declines significantly during the winter (for TL817729, chi-squared = 12.187, d.f. = 1, P < 0.001; for TL752760, chi-squared = 45.335, d.f. = 1, P < 0.001; for TL395629, chi-squared = 4.800, d.f. = 1, \dot{P} < 0.05). Similar declines in infestation rates during the winter are evident in the samples of C. 11-punctata from Hengistbury Head (SZ175905) in 1986/1987 and Coton (TL415596) in 1993/1994, and of H. 4-punctata from King's Forest (TL817729) in 1988/1989. Furthermore, in the samples of T. 16-punctata, taken each October and March from 1986 until 1989, from Mildenhall (TL752760), King's Forest (TL817729) and Dry Drayton (TL395629), although infestation rates are low, there is a consistent decrease in the proportion found to be parasitized over the winter.

There are five possible explanations for the decline through the winter in the proportions of samples that are parasitized. First, infected hosts may become active earlier in the spring than uninfected hosts, possibly being stimulated into early season foraging as a result of low nutrient reserves due to the parasitoid draining resources. Although not recorded for D. coccinellae, this effect has been noted from other members of the subfamily Euphorinae (Wylie, 1982). In this case, the decline may simply be a result of infected individuals leaving the main overwintering sites

before uninfected beetles.

Second, infected individuals may move away from other conspecifics to reduce the probability of uninfected ladybirds being attacked once the parasitoid emerges. Such altruistic behaviour has been reported in the pea aphid (A. pisum) parasitized by the

wasp Aphidius ervi (Hal.). Infected aphids "commit suicide" by dropping off their food plant. Their suicide decreases the probability of the parasitoid attacking their parental colony either because the wasp within them dies with them, or because they thereby remove the wasp to a safe distance from their parental colony (McAllister and Roitberg, 1987). In the case of ladybirds, movement to exposed positions, thereby increasing the probability of death from winter bird predation (Majerus & Majerus, in press) or climatic exposure, or to low herbage layers well removed from most overwintering aggregations, would reduce the likelihood of parasitized ladybirds being collected compared to unparasitized individuals. However, it is important to stress that such behaviour is only likely to evolve under kin selection. That is to say, the advantage from this suicidal behaviour of parasitized individuals accrues primarily to closely related ladybirds. While instances of such advantages have been reported in some aposematic species (Tostowaryk, 1971; Shapiro, 1976; Bowers, 1979) these cases involve species in which aggregations consist of siblings. This is not the case for most coccinellids, in which each winter aggregation probably involves a random selection of the local population.

Third, the parasitoids may induce behavioural changes in their hosts for their own benefit. For example, Brodeur & McNeil (1989) report that the wasp Aphidius nigripes modifies host behaviour depending on whether the wasp is entering diapause phase or not, to reduce the incidence of hyperparasitism. Similarly, the wasp *Cotesia* (= Apanteles sensu lato, in part) euphydryidis (Muesebeck), which parasitizes larvae of Euphydryas phaeton Drury, alters the behaviour of its host to increase its chances of escaping predation (Stamp, 1981). Several other cases of this kind have been reported (see Fritz, 1982 for review). In the case of ladybirds, it is not obvious what benefits parasitoids might gain by removing their hosts from their normal overwintering sites. Predation of coccinellids in overwintering aggregations by birds does occur, but is a relatively rare phenomenon (Majerus & Majerus, in press). Attacks on coccinellids by other predators or by parasitoids during the winter have not been documented. Consequently, it is difficult to conceive how removal of hosts from aggregations is likely to benefit the parasitoid if one concedes an adaptive explanation for aggregative overwintering in coccinellids. However, this negative argument does not say there is no benefit, simply that no benefit has yet been envisaged.

Fourth, the decline could be explained if parasites were to emerge from their hosts during the winter. This possibility can be reasonably rejected due to the weight of evidence showing that development of *D. coccinellae* is arrested in diapausing hosts (for example, see Kadono-Okuda *et al.*, 1995).

Finally, the parasitoid's drain on its host's resources may decrease the probability

of the host surviving through the winter.

Sequential samples taken throughout the winter, and experiments to test the mortality and dispersal behaviour of parasitized and unparasitized ladybirds during the winter, are needed to test these possibilities.

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BOOK REVIEW

Plant galls by Margaret Redfern and R. R. Askew. Naturalists' Handbooks 17, Richmond Publishing Co. Ltd., Slough, 1992. £16 hardback, £8.95 paperback, 99 pp.—Cecidology, the study of galls (from the Greek *kekis* a gall) is deservedly increasing in popularity in Britain. The activities of the British Plant Gall Society in promoting cecidology via their meetings and publications have now been augmented

by this well-illustrated and attractively produced guide.

An amazing amount of information is packed into the pages of this little book. Starting with an introduction which includes consideration of the definition and formation of galls, chapter 2 gives examples of the different agents responsible for inducing galls, and chapter 3 examines a good selection of the communities and interactions which are known for suites of insect galls on some familiar plants. The latter chapter concludes with a helpful table of suggestions for projects, which should stimulate keen readers to initiate their own original studies. Galls, their causers and associated species are ideal subjects for study; their life cycles, changing numbers over time, interactions between associated species, spatial distribution and natural enemies are all suitable for study by anyone with sufficient patience and persistence. Many galls are common and widely distributed, and will be found even in small gardens where their hostplants occur. Little equipment is needed for their study, though a binocular microscope is highly desirable for activities such as dissecting galls, counting and identifying their occupants, or examining the process of gall initiation and development. Chapter 4 on identification takes up half the book, and this enables the causers of galls on a selection of common plants to be identified to species. Sound advice on using other key works and getting vouchers confirmed by specialists will help those attracted to cecidology by this publication to get off to a good start. The inexpensive Provisional keys to British plant galls by F. B. Stubbs (1986), published by the British Plant Gall Society, which allows the majority of British gall-causers to be identified, is an ideal companion volume. However, Plant galls not only enables gall-causers to be studied, but also gives an entry to the intricate world of their predators, parasitoids and some other associated species, which are not included in any other general guide. A brief section on techniques. some useful addresses and six pages of references and further reading, together with an index, complete the book.

Given the range of technical terms used, a glossary might have been worth including to aid comprehension, but this is a small omission in a well-planned and stimulating introduction to this fascinating subject. The experience and enthusiasm of the authors for their field shines through and the result is one of the best of this consistently good series. Strongly recommended!

I. F. G. McLean